

Juvenile-mature Genetic Correlations in *Picea abies* (L.) Karst. Under Different Nutrient and Mycorrhiza Regimes

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Abstract

Genetic correlations and selection efficiency estimates were used to study the possibilities of early selection based on growth chamber performance. Results from two experiments with 30 open-pollinated families from a Swedish Norway spruce seed orchard grown in growth chambers were compared with field performance of 24-year old progenies from the same seed orchard. One of the two growth chamber experiments was a 2x2 factorial design combining two levels of nitrogen with the presence or absence of ectomycorrhizal symbiont, *Laccaria bicolor* (Maire) Orton over 18 weeks (Experiment 1). The objective was to study variation in nitrogen uptake. In the other experiment, seedlings from the same families were studied at two levels of nitrogen and phosphorus over 47 weeks (Experiment 2). The objective was to study variation in nitrogen and phosphorus utilization. The overall proportion of significant correlations between growth chamber traits and field traits was low, 7% and 25% for experiments 1 and 2, respectively. In experiment 1, low nitrogen treatment with mycorrhiza in the growth chamber gave the highest number of significant correlations with field traits, supporting the hypothesis that mimicking field conditions improves juvenile-mature correlations. In experiment 2, the high nitrogen treatment had the strongest juvenile-mature correlations, but most were negative. The significant J-M correlations were not evenly distributed over the three field trials. In both experiments, field data from one trial had strong J-M correlations but it was with different trials in the two experiments. Even though there were significant correlations of certain traits with field trials, the results were inconsistent without any satisfactory explanation for the inconsistency. It is thus too early to make recommendations for practical use based on the results.

Key words: *Picea abies*, growth chamber, mycorrhiza, genetic correlations, field trials.

Introduction

The time needed to test new varieties is one limiting factor in an efficient forest tree breeding programme. Normal field testing in Sweden takes 10–15 years which corresponds to 10–20% of normal rotation time. Reliable early testing methods would increase the genetic gain per unit time, which is one of the measures of profitability of tree improvement. The efficiency of early testing depends on the strength of the J-M genetic correlations, which in turn is dependent on the heritabilities of the juvenile and mature traits and the selection intensities at these two phases.

Important research has been carried out in recent years trying to reduce the time for reliable selection. However, ERIKSSON *et al.*, (1993), in their review of early tests in pines, reported rather conflicting results. Retrospective studies, where family performance is replicated in space and time, allow estimates of juvenile-mature (J-M) genetic correlations without measuring the same tree at different times. Such studies are designed

to discover early indicator traits (e.g. WILLIAMS 1988; LOWE and VAN BUIJTENEN, 1989; PHARIS *et al.*, 1991; LI *et al.*, 1992; SMITH *et al.*, 1993) and the optimal early test environments that will maximize the J-M genetic correlation (ERIKSSON *et al.*, 1993).

It is likely that stem volume in *Picea abies* under field conditions is a composite trait influenced by temperature conditions, water availability, and nutrient availability. So far, retrospective studies related to temperature and water availability have been carried out. DANUSEVICIUS *et al.* (1999) found generally poor correlations between growth chamber studies with imposed frost desiccation and results from mature field trials. In *Picea abies*, SONESSON *et al.* (2002) reported generally weak J-M correlations for the two temperature regimes tested, though the J-M correlations with periodic drought treatment in the growth chamber tests were somewhat stronger.

Since nitrogen is frequently growth limiting under Swedish forestry conditions (TAMM, 1991) it is possible that some adaptation to nutrient availability may have taken place. Nutrient efficiency probably depends on uptake of nutrients as well as their utilization in the production of biomass. Nutrient uptake has been shown to be strongly dependent on mycorrhizal associations (for a summary see SMITH and READ, 1997). There are J-M studies in *Picea abies* involving different temperatures and water availabilities (SONESSON *et al.*, 2002) but we are not aware of studies with different nutrient availabilities; there is thus a need to complement these studies.

The objective of this study was to use genetic correlations and selection efficiency estimates to study the potential of early selection by comparing traits in young seedlings under different nitrogen regimes with mature traits in 24-year old field trials.

Material and Methods

This study consisted of two experiments. The first, experiment 1, was designed to study genetic variation in N uptake at two levels of N in the presence or absence of ectomycorrhizal symbiont, *Laccaria bicolor*. In the second experiment, the objective was to study genetic variation in nitrogen and phosphorus utilization.

Material

Genetic background

The seed material in this study originates from a *Picea abies* seed orchard located at Maglehem in southern Sweden (55° 50'N, 14° 07' E, 60 m a s l).

Juvenile material, Experiment 1 – variation in nitrogen uptake

Seedlings from 30 open-pollinated families of *Picea abies* were transplanted at 6 weeks and seedlings that were designated to be mycorrhizal were inoculated with *Laccaria bicolor*. This was followed by 2 weeks of establishment during which

mycorrhizal and non-mycorrhizal seedlings were watered on 5 occasions to field capacity with either 25 mg N/L (low-N) or 200 mg N/L (High-N). They were then grown for 10 weeks at 20 °C with 3-hour nights, without any further supply of water or nutrients. The whole experiment was replicated four times to obtain sufficient material for statistical analysis. 4 x (30 families x 4 treatments x 5 blocks), giving a total of 2400 plants. Seedlings were arranged in a randomized complete block design in the growth chamber.

The ectomycorrhizal symbiont *Laccaria bicolor* (Maire) Orton, strain 238, from the laboratory of Prof. J. TRAPPE, Oregon State University, originally isolated under *Tsuga mertensiana* in Oregon, USA, was used for inoculation. This species was chosen because it grows at *Picea abies* sites in Sweden and infects roots of *Picea abies* successfully at relatively high soil nitrogen concentrations (WALLANDER and NYLUND, 1992). It has a prolific growth habit in culture and tolerates homogenization making it suitable for inoculum production for a large-scale genetic experiment. This experiment is described more detailed in MARI *et al.* (accepted a). The traits studied in Experiment 1 are shown in Table 1.

Table 1. – Description of traits studied in growth chamber experiments.

Abbreviation	Description	Unit	Experiment	
			1	2
RC	Length of elongated hypocotyls	mm	X	
MH	Height from cotyledon to terminal bud after 5 weeks	mm	X	
FH	Height from cotyledon to terminal bud after 10 weeks	mm	X	
WN	Weight of needles	g		X
H ₁	Height at the end of the first growth period	mm		X
H ₂	Height at the end of the second growth period	mm		X
HINC	Height increment	mm		X
SDW	Shoot dry weight	g	X	X
RDW	Root dry weight	g	X	X
TDW	Total dry weight	g	X	X
RSR	Root shoot ratio		X	X
NAMT	N amount in shoot (Expt. 1) or needles (Expt. 2)	mg	X	X
NCONC	N concentration	mg/g	X	X
NAC	Nitrogen acquisition capacity		X	
NU	Nitrogen utilization	g/mg		X
PAMT	P amount	mg		X
PCONC	P concentration	mg/g		X
PU	Phosphorus utilization	g/mg		X

Juvenile material, Experiment 2 – variation in nitrogen utilization

In this experiment 30 open-pollinated families from the same seed-lots as in experiment 1 were grown in growth chamber for two growth periods (47 weeks). Growth cessation was induced by gradual prolongation of the nights.

The total experiment comprised 1440 seedlings (30 families x 2 treatments x 24 blocks). For each treatment, there was one seedling per family per block with randomisation of the families in blocks. The two treatments were physically separated from each other in the growth chamber to allow for two different watering systems.

Two nutrient treatments were applied; one set of seedlings was given free access (High-N) and the other restricted access

to nutrients (Low-N). The High-N treatment consisted of irrigation with a balanced nutrient solution containing 100 mg N per litre. In the Low-N treatment, seedlings were fertilized according to the principles of INGESTAD (1979) – the nutrient supply increased with increasing size and demand of seedlings, i.e. the daily dose varied over time during the growth period. Traits assessed and abbreviations of the names are given in Table 1. This experiment is described more detailed in MARI *et al.* (accepted b).

Mature material

Three field progeny trials established in 1977 were used for this study (Table 2). The progenies were full-sib families from controlled crossings in the seed orchard. They were obtained from a partial diallell mating design with 7 crossings per

Table 2. – Field trial locations.

	Trial		
	775	779	783
Latitude	56° 26'	56° 40'	57° 25'
Longitude	14° 20'	13° 05'	15° 09'
Altitude (m)	150	90	210

parent. The trials were established with 3-year old seedlings and planted with 2x2 m spacing. The experimental design was 10 randomised complete blocks with single tree plots. Each full-sib family was represented by 4 seedlings in each block, in total 40 seedlings per family and trial. The trials have been assessed for different traits at three different times. Since only three blocks were measured at the last assessment, only field data for these trees were used for the analyses of field traits. The traits used in this study are described in Table 3.

Analysis

BLUP (Best Linear Unbiased Predictors) breeding values for material in field trials were obtained using the software VDIAL (DANELL, 1988). The same software was used to estimate components of variance and genetic correlation coefficients between traits within trials. Models for the analysis are described by KARLSSON and DANELL (1989).

BLUP-values for the two experiments with juvenile material were predicted using the “Mixed” procedure in SAS software (SAS, 1997). Description of analyses and genetic parameters from these experiments can be found in MARI *et al.*, accepted (a and b).

Pearson coefficients of J-M correlation between BLUP-values for the juvenile and mature material were estimated using SAS Proc Corr (SAS 1997).

The PEARSON J-M correlation coefficients were used to obtain genetic correlation coefficients (YAMADA, 1962), using the following formula:

$$r_G = \frac{r_{xy}}{(r_{TP_X} r_{TP_Y})}$$

Table 3. – Field trial traits used in the analysis.

Trait	Assessment Year	Trial		
		775	779	783
Height at age 13 or 14 (dm)	1986 or -87	H14(775)	H14(779)	H13(783)
Height at age 18 (dm)	1991	-	H18(779)	H18(783)
Height at age 21 (dm)	1994	-	H21(779)	H21(783)
Height at age 24 (dm)	1998	H24(775)	H24(779)	H24(783)
Increment between age 14 and 24 (dm)	Calculated	I(775)	-	-
Increment between age 18 and 24 (dm)	Calculated	-	I(779)	I(783)
Diameter of breast height, age 24 (mm)	1998	D24(775)	D24(779)	D24(783)
Volume/stem at age 24 (dm ³)	Calculated	V24(775)	V24(779)	V24(783)

Where r_{xy} is the PEARSON J-M correlation coefficient between BLUP-values, and r_{TPx} and r_{TPy} are the estimated correlation coefficients between the “true” and predicted clone values for traits x and y , respectively. r_{TP} for the growth chamber material is calculated as

$$\sqrt{\frac{h_A^2 k}{4 + h_A^2 (k - 1)}}$$

and for the field trials as

$$\sqrt{\frac{\sigma_A^2 - p_e^2}{\sigma_A^2}}$$

where h_A^2 is the individual tree (additive) heritability, k is the harmonic mean of the number of replications/family, σ_A^2 is the additive variance and p_e is average prediction error for the breeding values.

The relative efficiency (R_{xy}) of early selection for growth chamber traits was calculated as a gain ratio of the indirect selection in the growth chamber to the direct field trial selection as described in LAMBETH (1983):

$$R_{xy} = \left(\frac{i_x h_x}{i_y h_y} \right) r_g$$

where i_x is the selection intensity in x , h_x is the square root of heritability in x , i_y is the selection intensity in y , h_y is the square root of heritability in y and r_g is the genetic correlation between x and y . We assume that $i_x = i_y$.

Results

Mature material

The height and diameter development were similar for all sites. The heritability estimates were rather high for field trials, averaging 0.17 and do not vary much among trials for the same trait (Table 4).

Table 4. – Mean values, coefficients of additive variation (CV_A) and narrow sense heritabilities (h^2) for the analysed traits in different trials.

Trait (unit)	775			779			783		
	Mean	CV_A (%)	h^2	Mean	CV_A (%)	h^2	Mean	CV_A (%)	h^2
H13/14 (dm)	40.6	11.1	0.13	41.8	8.5	0.13	38.7	8.7	0.13
H18 (dm)	-	-	-	61.3	8.4	0.15	65.3	9.5	0.22
H21 (dm)	-	-	-	71.7	8.4	0.17	79.4	8.8	0.22
H24 (dm)	83.8	9.3	0.15	84.3	8.3	0.19	96.5	8.1	0.21
I15-24 (dm)	43.2	8.1	0.11	-	-	-	-	-	-
I19-24 (dm)	-	-	-	23.1	9.6	0.18	31.2	6.4	0.10
D24 (mm)	106.9	14.2	0.18	105.6	9.6	0.14	120.1	12.3	0.23
V24 (dm ³)	49.5	29.5	0.18	46.8	23.6	0.14	65.0	24.9	0.21

Juvenile material

Except for the High-N+mycorrhiza treatment, most traits in the other three treatments in Experiment 1 had high heritabilities (>0.20) (Table 5). The heritabilities of the traits in

Table 5. – Mean values and heritabilities for the traits studied in Experiment 1.

Trait	Low-N		Low-N+mycorrhiza		High-N		High-N+mycorrhiza	
	Mean	h^2	Mean	h^2	Mean	h^2	Mean	h^2
RC	34.4	0.76	35.2	0.50	34.1	0.46	35.3	0.42
MH	14.6	0.29	29.2	0.21	47.0	0.30	49.3	0.12
FH	44.3	0.28	66.0	0.30	87.9	0.27	100.2	0.23
RDW	0.13	0.31	0.22	0.19	0.30	0.28	0.35	0.10
SDW	0.14	0.41	0.28	0.32	0.56	0.29	0.69	0.11
TDW	0.25	0.43	0.48	0.30	0.84	0.33	1.02	0.10
RSR	1.10	0.19	0.85	0.04	0.55	0.13	0.53	0.00
NAMT	2.02	0.24	2.23	0.24	14.1	0.21	15.9	0.10
NCONC	15.2	0.16	8.05	0.25	26.8	0.30	24.0	0.00
NAC	0.15	0.47	0.17	0.19	-	-	1.20	0.25

Experiment 2 (Table 6) were generally higher than in Experiment 1. However, nitrogen amount (NAMT) and phosphorus amount (PAMT) in the Low-N treatment and root/shoot ratio in both treatments were characterized by low heritabilities.

Table 6. – Mean values and heritabilities for the traits studied in Experiment 2.

Trait	Low-N		High-N	
	Mean	h^2	Mean	h^2
WN	1.04	0.28	2.04	0.55
H ₁	41.8	0.45	101.0	0.82
H ₂	118.9	0.33	219.0	0.49
HINC	77.1	0.20	118.0	0.35
SDW	1.37	0.25	2.85	0.53
RDW	0.91	0.24	0.92	0.48
TDW	2.28	0.26	3.77	0.54
RSR	0.68	0.08	0.41	0.02
NAMT	11.5	0.05	48.0	0.58
NCONC	11.5	0.37	24.1	0.29
NU	0.33	0.28	0.09	0.08
PAMT	2.07	0.07	6.73	0.57
PCONC	2.06	0.23	3.47	0.19
PU	1.11	0.22	0.55	0.08

Genetic correlations and selection efficiency in Experiment 1

In total, there were 48 statistically significant correlation coefficients between BLUP-values out of 684 estimated (see Table 7). Trial 775 contributed 7 of these, trial 779 contributed 12 and trial 783 contributed 29. These 48 were evenly distributed over mycorrhizal and non-mycorrhizal treatments at each N level. Most of the significant correlations, 38, were found among the Low-N treatments. The absolute values of the mean correlation coefficients for the significant relationships

Table 7. – Number of significant juvenile-mature correlations obtained between traits in Experiment 1 and field data from three field trials (no. of sign. correlations/total no. of correlations) and the mean correlation coefficients for the significant relationships.

Treatment	Trial No. 775		Trial No. 779		Trial No. 783	
Low-N	3/50	-0.67 RSR (3)	3/70	-0.56 NAC (3)	13/70	-0.62 RDW (7)
	-	-	-	-	-	-0.77 RSR (6)
Low-N + mycorrhiza	0/45	-	3/63	+0.56 SDW (1)	16/63	+0.61 SDW (6)
	-	-	-	+0.62 NAMT (2)	-	+0.67 RDW (1)
	-	-	-	-	-	+0.64 TDW (3)
	-	-	-	-	-	+0.65 NAMT (6)
High-N	2/45	+0.58 MH (1)	3/63	+0.57RC (3)	0/63	-
	-	+0.75 NAMT (1)	-	-	-	-
High-N + mycorrhiza	2/40	-0.65 NAC (2)	3/56	-0.66 NAC (3)	0/56	-

varied in the range 0.56–0.77. The absolute values of the average selection efficiency for the combinations of treatments and traits with significant J-M correlations in trial 783 varied in the range 72–84 % (Table 8).

Table 8. – Average selection efficiency (%) of traits in the Low-N treatments (Experiment 1) with significant J-M genetic correlations with trial 783.

Treatment	SDW	RDW	TDW	RSR	NAMT
Low-N	-	-84	-	-81	-
Low-N + mycorrhiza	78	81	83	-	72

Genetic correlations and selection efficiency in Experiment 2

The total number of correlations estimated for this experiment and field trial traits was 532, of these 133 were significant (Table 9). The majority, 77, of the significant correlations was found in the high N-treatment. Ninety-nine of the significant correlations were found for traits in trial 779 while trial 775 and 783 contributed 15 and 19 significant correlations respectively. The mean correlation coefficients for the significant relationships varied in the same range as in Experiment 1. Notable were the significant but negative J-M correlation estimates with growth traits in the growth chamber. These were more pronounced for the High-N treatment. Rather strong positive correlations were found for NAMT, NCONC, and PCONC for Low-N treatment and for PCONC in the High-N treatment.

Table 9. – Average genetic correlation estimates for combinations of traits and treatments in Experiment 2 with significant J-M correlations. The number of significant correlations is given within brackets. The possible number of combinations were 70 for trial 775 and 98 in trials 779 and 783.

Treatment	Low-N			High-N		
Trial id.	775	779	783	775	779	783
No. of sig. correlations	13	36	7	2	63	12
Trait						
NW	-0.60 (1)	-	-	-	-0.65 (7)	-
H ₁	-	-0.58 (2)	-	-	-0.59 (6)	-
H ₂	-	-	-	-	-0.64 (7)	-
HINC	-	-	-	-	-0.54 (1)	-
SDW	-0.61 (1)	-0.57 (1)	-0.57 (3)	-	-0.64 (7)	-
RDW	-	-0.61 (2)	-	-	-0.66 (6)	-
TDW	-	-0.60 (3)	-0.59 (3)	-	-0.64 (7)	-
RSR	-	-	-	-	-	-
NAMT	-	1.08 (4)	-	-	-0.67 (7)	-
NCONC	0.56 (3)	0.65 (6)	-	-	-	-
NU	-0.61 (4)	-0.71 (6)	-0.54 (1)	-	-	-
PAMT	-	-	-	-	-0.64 (6)	-
PCONC	0.61 (2)	0.78 (6)	-	0.66 (1)	0.78 (6)	0.76 (7)
PU	-0.66 (2)	-0.76 (6)	-	-0.90 (1)	-0.78 (3)	-0.98 (5)

Table 10. – Average selection efficiency (%) for growth chamber traits with significant J-M genetic correlations in Experiment 2.

Treatment	Low-N			High-N		
Trait/Trial id.	775	779	783	775	779	783
NAMT	-	64	-	-	-131	-
NCONC	96	101	-	-	-	-

Discussion

If we consider only the proportion of significant correlations the results may seem discouraging. However, it is important to see whether there are some useful trends which could be studied further as part of a continued effort to develop early tests. Such an analysis should consider the variation among field trials, treatments, and the juvenile traits. It ought to be stressed that results from field trials are usually accepted as

the ‘genetic truth’ of the material involved. However, it must be remembered that there are various kinds of imperfections related to field trials that may influence J-M correlations. Pollen contamination during extraction and pollination, as well as within-site heterogeneity are two examples of such imperfections. Finally, it should be mentioned that some correlations are strong owing to a very small denominator, which was the case for NAMT in its correlation with field traits in trial 779 (Table 9). It is also worth noting that trait – trait family mean correlations between experiment 1 and 2 were generally poor, because the two experiments were designed to achieve different objectives (see materials and methods) this suggests that different sets of genes regulate the traits in nutrient uptake (experiment 1) and nutrient utilization (experiment 2).

Experiment 1

It is expected that 5% of the correlations may be significant for random reasons. As seen from Table 7, it may be concluded that the number of significant correlations for the two High-N treatments is so low that random reasons could explain their occurrence. With 783 and the two low-N treatments the number of significant J-M correlations is so large that random reasons may be ruled out as an explanation. This calls for an analysis of the differences between trial 783 and the other two trials. The mean stem volume in this trial is at least 24% larger than in the two other trials (Table 4) in spite of the fact that it is located in a harsher climatic region than the other two trials. Heritabilities were mostly higher in trial 783 than in the two other trials. The heritabilities of the field traits in trials 775 and 779 are not so low that they constitute a constraint to strong J-M correlations. The differences are not large but may be large enough to allow the correlations to pass the border of significance for trial 783 although not for the two other trials.

It is of significance that the Low-N+mycorrhiza treatment, which most closely mimics the field situation, had the highest number of significant J-M correlations. The results from this experiment give some support to the hypothesis that mimicking field conditions in juvenile experiments could improve the J-M relationship (cf Introduction). The shoot dry weight of seedlings with Low-N was half of the value in the Low-N+mycorrhiza treatment. This is a drastic reduction and it may be speculated that a somewhat higher N-dose than the 25 mg/L given in the Low-N+mycorrhiza treatment would mimic field conditions better with improvement of the J-M correlations as a result.

The high proportion of significant correlations for NAMT and SDW in the Low-N+ mycorrhiza treatment (8/19 and 7/19) suggests that nitrogen uptake and shoot dry weight in such a type of experiment are fairly good predictors of future growth.

Experiment 2

Trial 779 dominated the significant J-M correlations. In contrast to the previous experiment trial 779 had more significant correlations in the High-N treatment than in the Low-N, 63 versus 36. Moreover, for all growth-related traits, significant J-M correlations were negative in both treatments (Table 9), which means that the best growing families in the juvenile material were smallest in field. Such a negative relationship between juvenile and mature growth is hard to explain. One possible reason may be that the juvenile growth to a large extent can be attributed to free growth (cf EKBERG *et al.*, 1991). Since free growth is a juvenile trait that disappears with age (cf. VON WÜHLISCH and MUHS, 1986) it is at least theoretically possible that this trait is negatively correlated with predetermined growth. This would result in negative J-M correlations

of growth traits. Free growth is also promoted by non-limiting growth conditions (VON WÜHLISCH and MUHS, 1991). This may explain the higher number of significant J-M correlations in the High-N treatment. SONESSON *et al.* (2000) in their growth chamber studies with *Pinus sylvestris* L. reported some negative and significant J-M correlations between root weight and field stem volume. They concluded that it might be attributed to differences in allocation of biomass. Such an explanation is not valid for our material with significant and negative J-M correlations for above-ground biomass traits.

In both treatments phosphorus concentration had many positive significant correlations with field growth in trials 779 and 783 (High-N only) while nitrogen concentration was significantly correlated in the Low-N treatment only in trial 779. Shoot dry weight in the Low-N treatment was approximately half of that in the High-N treatment (Table 6). As suggested for experiment 1 it would be worthwhile to use a somewhat higher level of nutrient availability in future studies of nutrient utilization.

General discussion

Our results agree with results reported for the same *Picea abies* families studied in a factorial temperature and water availability experiment by SONESSON *et al.* (2002). They reported significant correlations mainly with one field trial, 783, and not with others. DANUSEVICIUS *et al.* (1999) reported weak J-M correlations when comparing early heights after simulated frost desiccation for seedlings of the same families as used in our study with field performance. We know of no early tests with *Picea abies* involving different nutrient regimes. A study on nitrogen and phosphorus utilization with *Picea sitchensis* carried out by our group resulted in weak and non-significant J-M correlations. One of the reports with the highest J-M correlations (ERIKSSON *et al.*, 1993) showed that the strongest correlations were obtained with growth data from age 28, when the competition had started. The low number of significant correlations in our study cannot be attributed to too young field material since the trees in our field trials were larger than the *Pinus sylvestris* trees in the study by ERIKSSON *et al.*, (1993).

It is likely that tree growth in the field trials involved in our study is limited by several factors such as temperature, nutrient use efficiency, water use efficiency, and photosynthesis efficiency. Nutrient use efficiency can be split into nutrient uptake, nutrient utilization and nutrient translocation (ERIKSSON, 1998). It is likely that these factors interact in a complex way; temperatures may thus be the limiting factor one year while nutrient uptake is limiting another year. Only under conditions when one of the external factors is totally dominating for field tree growth over all years we can expect to obtain really strong J-M correlations by mimicking this growth limiting factor in the study of the juvenile material. Low, and in some cases negative, correlations between height in the growth chamber and growth in the field trials (Table 9) indicate that early selection for height would not be very efficient. Nor is it attractive to select for poor growth in growth chamber to obtain good field performance as is suggested by the data from experiment 2.

The selection efficiencies (Tables 8 and 10) were calculated without any consideration of the gain in time connected with

early testing. Considering also the potential gain in time, the significant correlations are satisfactorily high to make improvements in breeding. However, it is too early to make recommendations for practical use due to the inconsistencies with strong J-M correlations with field data from one trial but not with other trials. Future studies with higher nutrient availability than in the Low-N treatments of our two experiments are recommended.

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References

- DANELL, Ö.: VDIAL – A computer programme for univariate variance/covariance estimation BLUE/BLUP in diallel mating designs with fixed blocks (Manual in Swedish). The Institute for Forest Improvement, Uppsala, Sweden (1988). — DANUSEVICIUS, D., JONSSON, A., ERIKSSON, G. and KARLSSON, B.: Juvenile-mature genetic correlations after simulated frost desiccation in seedlings of *Picea abies* (L.) KARST. *Baltic Forestry* **5**, 19–27 (1999). — EKBERG I., ERIKSSON, G. and NILSSON, CH.: Consistency of phenology and growth of intra- and interprovenance families of *Picea abies*. *Scand. J. For. Res.* **6**, 323–333 (1991). — ERIKSSON, G.: Evolutionary forces influencing variation among populations of *Pinus sylvestris*. *Silva Fenn.* **32**, 173–184 (1998). — ERIKSSON, G., JONSSON, A., DORMLING, I., NORELL, L. and STENER, L.-G.: Retrospective early tests of *Pinus sylvestris* L. seedlings grown under five nutrient regimes. *Forest Sci.* **39**, 95–117 (1993). — INGESTAD, T.: Nitrogen stress in birch seedlings. II N, P, K, Ca, and Mg nutrition. — *Physiol. Plant.* **45**, 149–157 (1979). — LAMBETH C. C.: Early testing – overview with emphasis on loblolly pine. *Proc. South. For. Tree Improv. Conf.* **17**, 297–311 (1983). — LI, B., WILLIAMS, C. C., CARLSSON, W. C., HARRINGTON, C. A. and LAMBETH, C. C.: Gain in short-term testing: experimental results. *Can. J. For. Res.* **22**, 290–297 (1992). — LOWE, W. J. and VAN BULJTENEN, J. P.: The incorporation of early testing procedures into an operational tree improvement program. *Silvae Genet.* **38**, 243–250 (1989). — MARI, S., JONSSON, A., FINLAY, R., ERIKSSON, T., KAHR, M. and ERIKSSON, G.: Genetic variation in nitrogen uptake and growth in mycorrhizal and non-mycorrhizal *Picea abies* (L.) KARST Seedlings. Accepted (a) for publication in *Forest Science*. — MARI, S., JANSSON, G. and JONSSON, A.: Genetic variation in nutrient utilization and growth traits in *Picea abies* seedlings. Accepted (b) for publication in *Scandinavian Journal of Forest Research*. — PHARIS, R. P., YEH, F. C. and DANCİK, B. P.: Superior growth potential in trees: What is its basis, and can it be tested at an early age? *Can. J. For. Res.* **4**, 368–374 (1991). — SAS Institute Inc.: SAS/STAT Software. Changes and Enhancement through Release **6.12**. SAS institute Inc. Cary, N.C (1997). — SMITH, C. K., WHITE, T. L., HODGE, G. R., DURYEA, M. L. and LONG, A. J.: Genetic variation in first-year slash pine shoot components and their relationship to mature field performance. *Can. J. For. Res.* **23**, 1557–1565 (1993). — SMITH, E. S. and READ, D. J. (eds.): *Mycorrhizal symbiosis* 2nd edition. Academic Press, London (1997). — SONESSON, J., JANSSON, G. and ERIKSSON, G.: Retrospective genetic tests of *Pinus sylvestris* L. in growth chambers with two irrigation regimes and two temperatures. *Scand. J. For. Res.* **16**, 21–29 (2000). — SONESSON, J., JANSSON, G. and ERIKSSON, G.: Retrospective genetic testing of *Picea abies* under controlled temperature and moisture regimes. *Can. J. For. Res.* **32**, 81–91 (2002). — TAMM, C. O.: Nitrogen in terrestrial ecosystems. Questions of productivity, vegetational changes, and ecosystem stability. *Ecol. Studies* **81** (1991). — WALLANDER, H. and NYLUND, J. E.: Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. *New Phytol.* **120**: 495–503 (1992). — WILLIAMS, C. G.: Accelerated short-term genetic testing for loblolly pine families. *Can. J. For. Res.* **18**, 1085–1090 (1988). — VON WÜHLISCH, G. and MUHS, H.-J.: Influence of age on sylleptic and proleptic free growth of Norway spruce seedlings. *Silvae Genet.* **35**, 42–48 (1986). — VON WÜHLISCH, G. and MUHS, H.-J.: Environmental influences on juvenile shoot growth in *Picea abies*. *Scand. J. For. Res.* **6**, 479–498 (1991).